**Potential nesting habitat for White-headed Woodpecker in Deschutes and Fremont-Winema National Forests**

(FINAL)

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by

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*Summary*

We identified potential nesting habitat for White-headed Woodpecker (WHWO; *Picoides albolarvatus*) within the Deschutes and Fremont-Winema national forests to inform forest management strategies and conservation planning. We developed and applied habitat suitability models calibrated with nest location data (*n* = 365) from the Chemult and Sisters ranger districts to accomplish this task. A previous model (Hollenbeck et al. 2011) was developed using nest location data (*n* = 382) from a relatively restricted portion of these sites. This model was less able to predict nest locations found during subsequent surveys that sampled a broader spatial extent. We therefore calibrated new models using both the original data and the more spatially extensive (but less numerous) data collected in subsequent surveys (Figure 1). When developing models, we considered 7 habitat variables describing various aspects of topography and forest structure (Table 1) thought to be important for nesting WHWOs (Wightman et al. 2010, Hollenbeck et al. 2011). We developed a partitioned Mahalanobis model (Rotenberry et al. 2006) and a Maxent model (Phillips et al. 2006) using subsets of these variables that optimized model performance. Using procedures specific to each technique, we ensured models were shaped equally by the original data and the new data despite differences in sample size. Models generated habitat suitability indices (HSIs) describing the relative suitability on a 0−1 scale (HSIs = 0 indicate minimal suitability; HSIs = 1 indicate maximum suitability) of 30×30-m pixels (see model descriptions below for their particular definitions of habitat suitability) HSIs from both models discriminated nest sites from background pixels representing available environmental conditions reasonably well and assigned similar HSI values to original versus recently collected data (Table 2). Substantial portions of the study area were consistently characterized by both models as being equally suitable to locations where nests occurred, but models also disagreed on the relative suitability of some areas (Figure 2). Mahalanobis and Maxent models derive alternative paradigms that are both valid. Additional research is needed to test the relative merits of these models and their respective paradigms for general characterization of WHWO nesting habitat. Meanwhile, land considered suitable by both models (i.e., where suitability is robust to variation in modeling paradigm and therefore more certain) is a judicious estimate of nesting habitat suitability. We suggest that future monitoring should aim to improve knowledge of WHWO habitat relationships in areas where models disagree. We provide spatially explicit HSI values and nest locations within Deschutes and Fremont-Winema forest boundaries in the accompanying geodatabase. We also describe how one can translate HSI values (i.e., relative indices of suitability) into more easily interpretable suitability classes comparable between models.

*Methods: model descriptions and evaluation*

Partitioned Mahalanobis $D^2$ models (Rotenberry et al. 2006) describe standardized environmental distances (re-scaled to a 0−1 range) from the multivariate mean for species presence locations (here, nest locations). Thus, these models defined habitat suitability as highest in environments most similar to the average environmental conditions where nests were located. Using a principal components analysis, we partitioned the environmental variance among nests, and HSIs were derived from those partitions for which nest HSIs varied the least (Rotenberry et al. 2006). We used re-sampling to balance the contribution across four nest location datasets: 1) original data within the Deschutes NF ($n$ = 231) and 2) the Fremont-Winema NF ($n$ = 96) (subset of nests used by Hollenbeck et al. 2011); 3) validation data from the Deschutes NF in 2010 ($n$ = 22), and 4) from the Fremont-Winema NF in 2011($n$ = 16) (Figure 1). We re-sampled the data 100 times, each time drawing 90 nests from each dataset (sampling with replacement from datasets with < 90 nests), and fitted Mahalanobis models to the re-sampled data. We initially constructed models using each variance partition derived from every combination of the seven habitat variables (one partition per variable in each combination) constrained to include variables of known importance (PIPO, ED, and SLP; Table 1; for importance of habitat features represented by these variables, see Wightman et al. 2010, Hollenbeck et al. 2011). From the 31 candidate models generated, we selected a model based on two performance metrics. A high median HSI value for nest locations indicated a relatively constrained nest distribution and was therefore desirable from a model selection perspective (Rotenberry et al. 2006). We also calculated AUC (area under the receiver-operating curve; Fielding and Bell 1997) to evaluate the ability of models to discriminate nest locations from a sample of 10,000 background pixels. Background pixels were drawn at random but equally from the four areas sampled by each of the four datasets. We applied 5-fold cross-validation to each of the re-sampled datasets (i.e., identified 5 equally sized subsets and ran the model 5 times, withholding a different subset each time) and calculated the median nest HSI and AUC for each of the 500 cross-validation datasets (data withheld during calibration). We selected the model with the highest median nest HSI averaged across the cross-validation datasets (i.e., the mean of the median HSIs), and we examined AUC to verify the selected model's discriminative ability. When mapping model predictions, we averaged HSIs across models fitted to the 100 re-sampled datasets without cross-validation. We plotted summary statistics (mean ± 1 s.d.) of HSIs with environmental variables (i.e., dose-response plots; Hanser 2011) to examine relationships between habitat suitability and variables that contributed to the selected Mahalanobis model.

Maxent (maximum entropy) models describe the distribution of species-occupied pixels constrained to be maximally similar to the distribution of "background" pixels across a landscape of study (i.e., available habitat) (Elith et al. 2010). Based on this distribution, Maxent calculates a probability of presence conditional upon the available environmental distribution. For Mahalanobis models, we calibrated Maxent models giving equal weight to the four data subsets. Instead of resampling the nest data, however, we drew the 10,000 background pixels used for model calibration from the four areas sampled by the data subsets (Figure 1) in proportion to their sample sizes. Thus, we drew 6,352 pixels from the area within Deschutes NF sampled by the original data, 2,572 pixels from the area within Fremont-Winema NF sampled by the original data, 656 pixels from the area within Deschutes NF sampled by the recent data (2010), and 420 pixels from the area within Fremont-Winema NF sampled by the recent data (2011). By drawing background pixels in proportion to sampling effort, the Maxent algorithm factors out effects of biased sampling effort on habitat suitability estimates. Maxent models allow for a variety of possible species-habitat relationships (linear, quadratic, interactive, threshold, and hinge

relationships) with habitat variables. The Maxent algorithm weights particular relationships to balance model fit and complexity with generality, and thus relaxes the need for formal model selection. Nevertheless, use of a minimum number of variables (i.e., excluding extraneous variables and more than one of any group of highly correlated variables) is recommended (Elith et al. 2010). We therefore excluded variables that contributed minimally to an initially fitted model (as reported by the Maxent software). As for the Mahalanobis model, we used a version of the selected Maxent model fitted to all available data without cross-validation when mapping HSIs, and we used dose-response plots (Hanser 2011) to examine HSI relationships with contributing variables.

*Results*

Three-hundred and sixty-five nests were used to calibrate habitat suitability models. GNN data were not available for 19 of the 446 nests and there were 62 instances of a pixel containing > 1 nest, leaving 365 data points for modeling. The selected Mahalanobis model derived from the first variance partition arising from all variables except COSASP (median HSI = 0.633 averaged across 500 cross-validation datasets). The selected Maxent model included LocCC, SLP, ED, and PIPO as explanatory variables. Both models performed reasonably well at discriminating nest pixels from available background pixels, and HSI values for the original versus recently collected data were similar (Table 2). The two models consistently identified substantial portions of the landscape as relatively suitable for nesting WHWO, but the models also disagreed in some areas (Figure 2). Differences between models arose from differences in contributing variables and habitat relationships described with those variables (Figures 3, 4).

*Discussion: Interpretation of models for habitat conservation*

Without fully understanding the mechanistic reasons for all observed nest habitat relationships and without identifying a particular ecological question of interest, we cannot definitively evaluate the validity of any single habitat suitability model. Consequently, we developed two models derived from different paradigms to make inferences. Mahalanobis models arise more directly from ecological niche theory (Rotenberry et al. 2006), whereas Maxent models arise from resource selection theory (Phillips et al. 2006, Elith et al. 2010). Both approaches are valid from a theoretical perspective and have proven themselves effective relative to other techniques (Elith et al. 2006, Tsoar et al. 2007). Indeed, despite their different approaches, the two models described surprisingly similar habitat suitability maps when viewed at a coarse scale. Differences in model structure and emphasized habitat relationships, however, resulted in subtle, fine-scale differences in the location of low-suitability pockets within broad areas generally described as suitable. Because of our limited understanding of the mechanisms behind observed habitat relationships (e.g., why WHWO favor flat topography), we cannot evaluate which model best describes habitat relationships that are most accurate at fine spatial scales and most generally applicable. In areas consistently characterized as suitable by both models, however, predicted suitability is robust to some uncertainty regarding assumed habitat relationships. Thus, habitat conservation efforts should be focused in these areas. In contrast, management activities that may negatively impact WHWO should be focused in areas consistently characterized as unsuitable by the models. Future research can focus on verifying the predictive value of these models, particularly in areas where the two models disagree.

Habitat suitability models only describe suitability in relative terms, so interpretation of HSIs will require additional analysis. Often, continuous HSI values are translated into binary

classifications (unsuitable versus suitable) by identifying a classification threshold that optimizes some function of sensitivity (the proportion of used locations correctly classified as suitable) and specificity (the proportion of unused or available locations classified as unsuitable) (Liu et al. 2005, Franklin 2009). Use-availability data (e.g., our data) can only assess specificity with respect to available habitat, which includes both suitable and unsuitable habitat, so classification thresholds should emphasize sensitivity, although some specificity is necessary to make informative inferences. The above approach is ultimately based on relating HSIs to the prevalence of nest location data used to calibrate models. Alternatively (and more desirably), HSI values could be related to demographic parameters estimated with independent data (e.g, nest survival, Shaffer 2004, or occupancy rates corrected for imperfect detection, MacKenzie et al. 2006) to identify useful classification thresholds. Regardless, HSI values should be related to some attribute of management interest to translate model predictions into meaningful guidelines for managers.

*Literature cited*


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Table 1. Variables considered for development of habitat suitability models (either Maxent or Mahalanobis $D^2$) for nesting White-headed Woodpeckers. Habitat variables were derived from Gradient Nearest Neighbor (GNN) data. All variables were extracted at 30×30-m pixel resolution.

| Variable name (abbreviation) | Description | Variables included in selected models |
|---|---|---|
| Slope (SLP) | pixel slope in % rise over run | both |
| Cosine Aspect (COSASP) | pixel cosine-transformed orientation of slope (unitless) | neither |
| Local-scale canopy cover (LocCC) | percent canopy cover for 1-ha (3×3-cell) neighborhood | Maxent |
| Landscape-scale canopy cover (LandCC) | percent canopy cover for 314 ha (1-km-radius) neighborhood | Mahalanobis |
| Ponderosa pine (PIPO) | Percent ponderosa-pine-dominated forest for 314 ha (1-km-radius) neighborhood | both |
| Density large trees (TPH) | Number of large trees (> 50 cm dbh) within 1 ha neighborhood. | Mahalanobis |
| Edge density (ED) | Length of edge between alternate patch types characterized according to canopy cover class (0-10%, 10-40%, and 40-80%) within 314 ha (1-km-radius) neighborhood. | both |

Table 2. Performance of Maxent and Mahalanobis $D^2$ models describing habitat suitability for nesting White-headed Woodpeckers in the Deschutes and Fremont-Winema National Forests, Oregon. AUC evaluates model ability to discriminate nest from available locations. AUC between 0.5 and 0.6 generally reflects low accuracy, 0.6–0.8 reflects moderate accuracy, and >0.8 indicates excellent accuracy (cf. Phillips et al. 2006). Median HSIs (habitat suitability indices; $25^{th}$ and $75^{th}$ median-unbiased percentiles in parentheses) are reported for all nests ($n$ = 427), including nests located within the original spatial extent ($n$ = 389) and the broader spatial extent surveyed more recently ($n$ = 38). AUCs were averaged across 500 validation datasets withheld from calibration of replicate models.

| Model | AUC | median HSI for all data | median HSI for original data | median HSI for recent data |
|---|---|---|---|---|
| Mahalanobis | 0.67 | 0.63 (0.38, 0.83) | 0.64 (0.40, 0.83) | 0.59 (0.16, 0.79) |
| Maxent | 0.72 | 0.55 (0.42, 0.67) | 0.56 (0.43, 0.67) | 0.50 (0.38, 0.58) |

Figure 1. Nest location data and areas surveyed that encompass the four data subsets. The red circles comprise the areas surveyed originally (Hollenbeck et al. 2011) and grey circles are the data collected within these areas. Black areas are the more extensive areas surveyed for recently collected data (white circles). National Forest boundaries are depicted in green. Habitat data were not available for 81 of the 446 nests depicted in these figures, so those nests were not used to calibrate habitat suitability models.

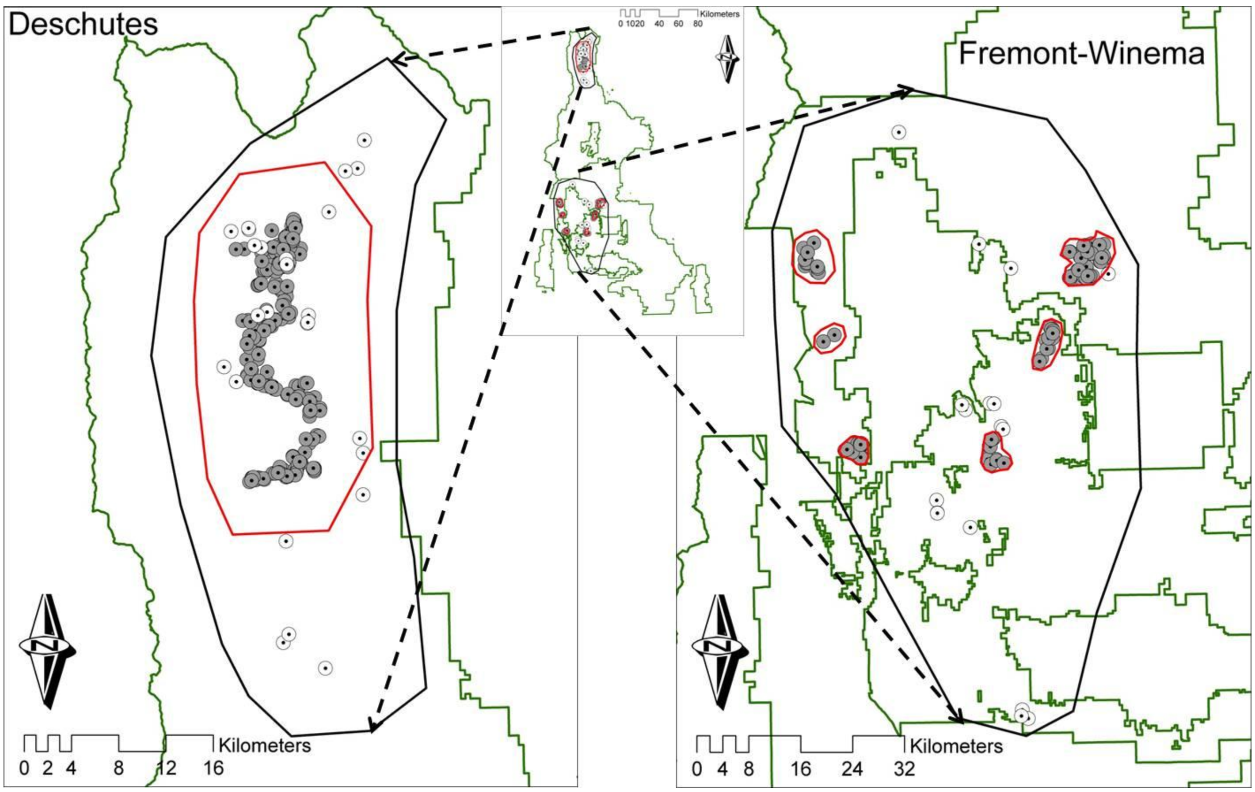

Figure 2. Habitat suitability maps derived from Mahalanobis $D^2$ (A) and Maxent (B) models. HSI values range from 0.0 (black), indicating minimal suitability, to 1.0 (white), indicating maximal suitability.

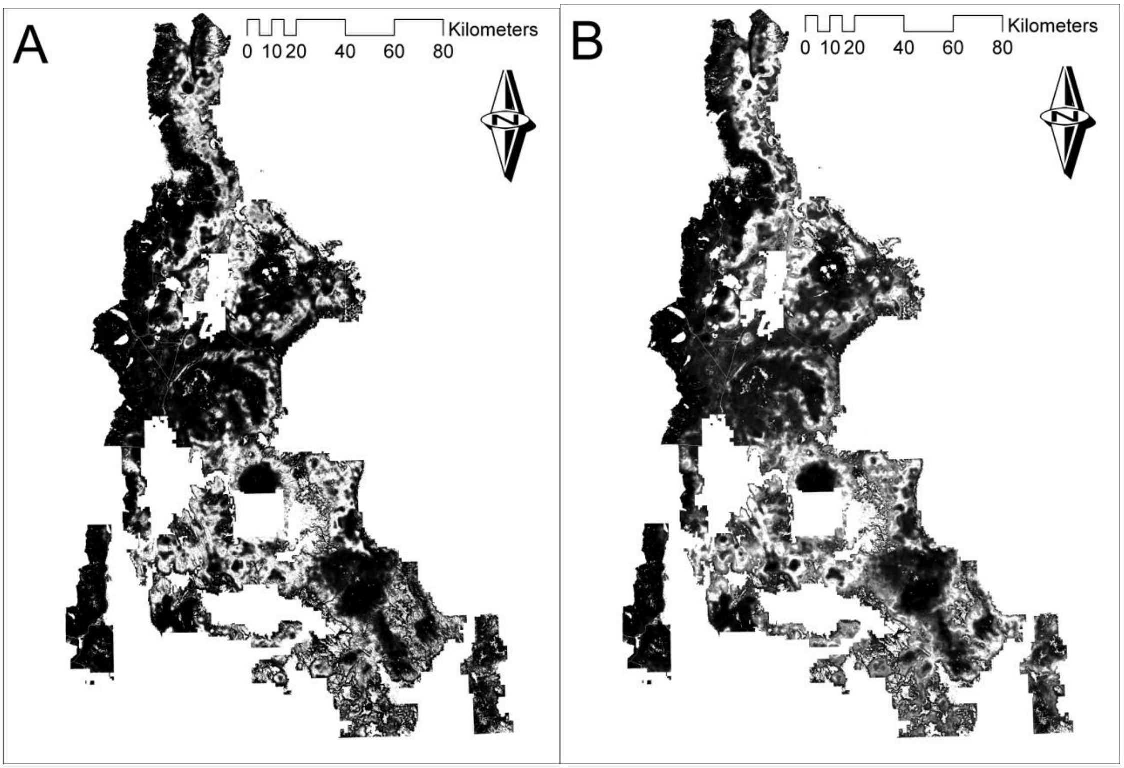

Figure 3. Dose-response plots (mean ± s.d. HSI plotted in relation to contributing variables) for the Mahalanobis $D^2$ model.

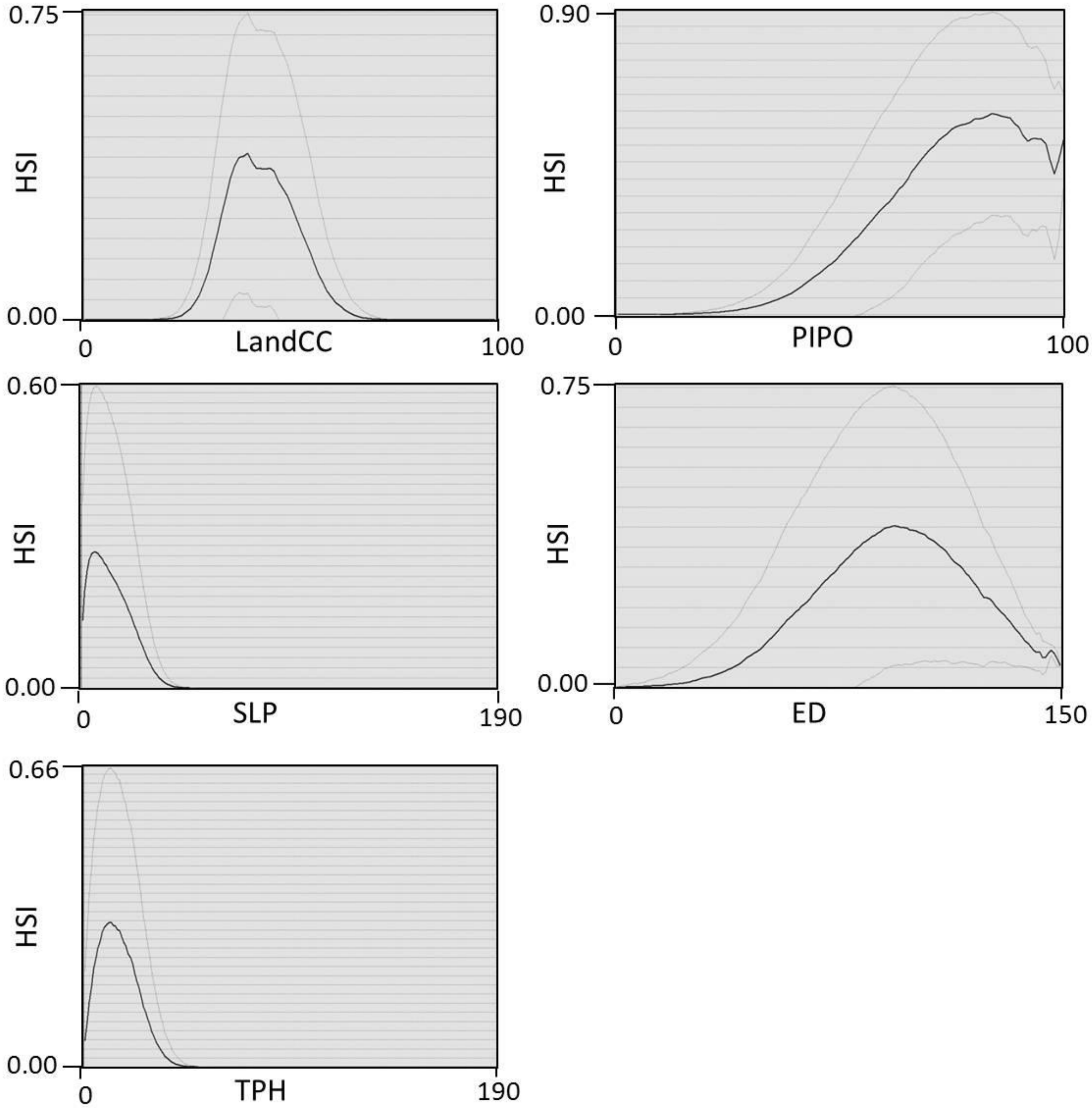

Figure 4. Dose-response plots (mean ± s.d. HSI plotted in relation to contributing variables) for the Maxent model.